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PARASITIC ORGANISMS IN THE BLOOD OF ARVICOLINE RODENTS IN ALASKA

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ABSTRACT: A *Grahamella*-like organism (Schizomycetes: Bartonellaceae) was found in erythrocytes of laboratory-reared northern voles, *Microtus oeconomus* Pallas, which had been inoculated intraperitoneally with a saline suspension of ground fleas, *Megabothris abantis* (Roths.), from wild northern voles captured at Lower Ugashik Lake, Alaska Peninsula. A live-trapped northern vole from the same locality harbored trypanosomes referable to *T. microti* (Mastigasida: Trypanosomatidae). Two morphologically similar but biologically different strains of piroplasms (Piroplasmasida: Theileriidae) of uncertain generic status were isolated from northern voles of Ugashik Lake origin and from northern red-backed voles, *Clethrionomys rutilus* Pallas, from the vicinity of Anchorage, Alaska. In the natural host, these piroplasms seemed to reproduce principally by schizogony in the spleen and bone marrow, but inexperimentally infected hosts from populations occurring outside the enzootic area, intraerythrocytic fission was a common method of reproduction. The vector of these piroplasms is evidently a tick, *Ixodes angustus* Neumann, whose geographic distribution in Alaska coincides with that of piroplasm-induced splenomegaly in arvicoline rodents. The piroplasms have been successfully transmitted from host to host in the laboratory via ticks of this species.

An organism resembling *Grahamella* spp. (Schizomycetes: Bartonellaceae), a trypanosome of the *T. lewisi* group (Mastigasida: Trypanosomatidae), and two piroplasms (Piroplasmasida: Theileriidae) of uncertain status have been found by us in arvicoline rodents in Alaska. We know of only one previous record of blood parasites from such rodents at high latitudes (Quay, 1955). The finding of *T. lewisi* in Norway rats, *Rattus norvegicus* (Berkenhout), by Schiller (1956) comprises the only other record of hematozoa in Alaskan rodents.

The present study developed from the investigation of an irruption of voles and lemmings on the Alaska Peninsula during the summer and autumn of 1963. Of unusual interest was the marked splenomegaly observed in a high proportion of the animals. Several pathogenic or potentially pathogenic organisms were isolated from these rodents in 1963 and in subsequent investigations in the same area in 1965. These included a bacterium, *Pasteurella tularensis*, and a spirochete, *Leptospira* cf. *ballum* (Rausch et al., 1969; Woods, unpublished), in addition to the four blood parasites mentioned above. The piroplasms were eventually found to be the causative agents of the splenomegaly. The tick *Ixodes angustus* Neumann probably is the vector of these organisms under natural conditions.

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The purpose of this paper is to report some findings concerning identification, occurrence, and geographic distribution of the parasites. The developmental cycle and pathogenicity of the piroplasms will be considered in greater detail elsewhere.

MATERIALS AND METHODS

Thin smears were prepared with blood drawn from the tail or toes of living voles and lemmings and from the axillary vein of the same individuals at necropsy. Spleen impression smears were prepared from these, as well as from snap-trapped animals. The preparations were air dried, fixed in absolute methanol, and stained by the Wright–Giemsa method. The animals were examined also for ectoparasites. All experimental animals utilized in this investigation were laboratory-born and -reared; most were of known ancestry. Inoculations were intraperitoneal, with sterile, citrated, phosphate-buffered saline or modified Alsever's solution utilized as a diluent for the blood and organ suspensions.

RESULTS

Grahamella-like organism

Minute, deeply staining rods, resembling organisms identified as *Grahamella* spp. by several investigators (e.g., Lavier, 1921; Carini and Fonseca, 1941; Tyzzer, 1942; Baker et al., 1963), were found within erythrocytes in thin smears of blood from northern voles, *Microtus oeconomus* Pallas, which had been inoculated with a suspension of ground fleas. The fleas, *Megabothris abantis* (Roths.), were obtained

from northern voles trapped at Lower Ugashik Lake (57°35′ N, 157° W), Alaska Peninsula, in October 1965. After storage alive in a glass vial for 2 days, the fleas were ground in 1 ml of saline, and 0.1 ml of this suspension was injected into each of three laboratory-reared voles. Four siblings of the experimental animals were inoculated with a suspension of ticks, *Ixodes angustus* Neumann, from the trapped voles, and eight white mice, *Mus musculus* L. (strain HA/ICR), received the remainder of the flea suspension. Smears of peripheral blood were prepared from the voles at irregular intervals from the 6th to the 99th day after inoculation; smears were prepared from the mice only on the 23rd day.

On the 6th day following inoculation, two to five *Grahamella*-like bodies, about 1 to 1.25 μ long by 0.25 μ wide, were found in the cytoplasm of each of a few erythrocytes from the voles which had received the flea inoculum. By the 17th day, about 6% of their erythrocytes were infected with from 6 to 14 organisms per cell (Fig. 1). The number of organisms and percentage of cells infected had diminished by the 23rd day, and none was found thereafter. None of the smears from voles receiving the tick inoculum nor those from mice receiving the flea inoculum showed intraerythrocytic bodies of this kind. Neither were any *Grahamella*-like organisms found in smears (19th day) from two northern voles inoculated earlier (October 1963) with a suspension of 21 fleas (*M. abantis*) from voles taken in the same area.

Tentative identification of the organisms as *Grahamella* sp. was based on their form, staining properties, occurrence within (rather than on) the erythrocytes, and on the brief duration of their invasive stage in the erythrocytes. Further study, by use of splenectomized animals or by culture of the organisms in vitro (Tyzzer, 1942), was not feasible.

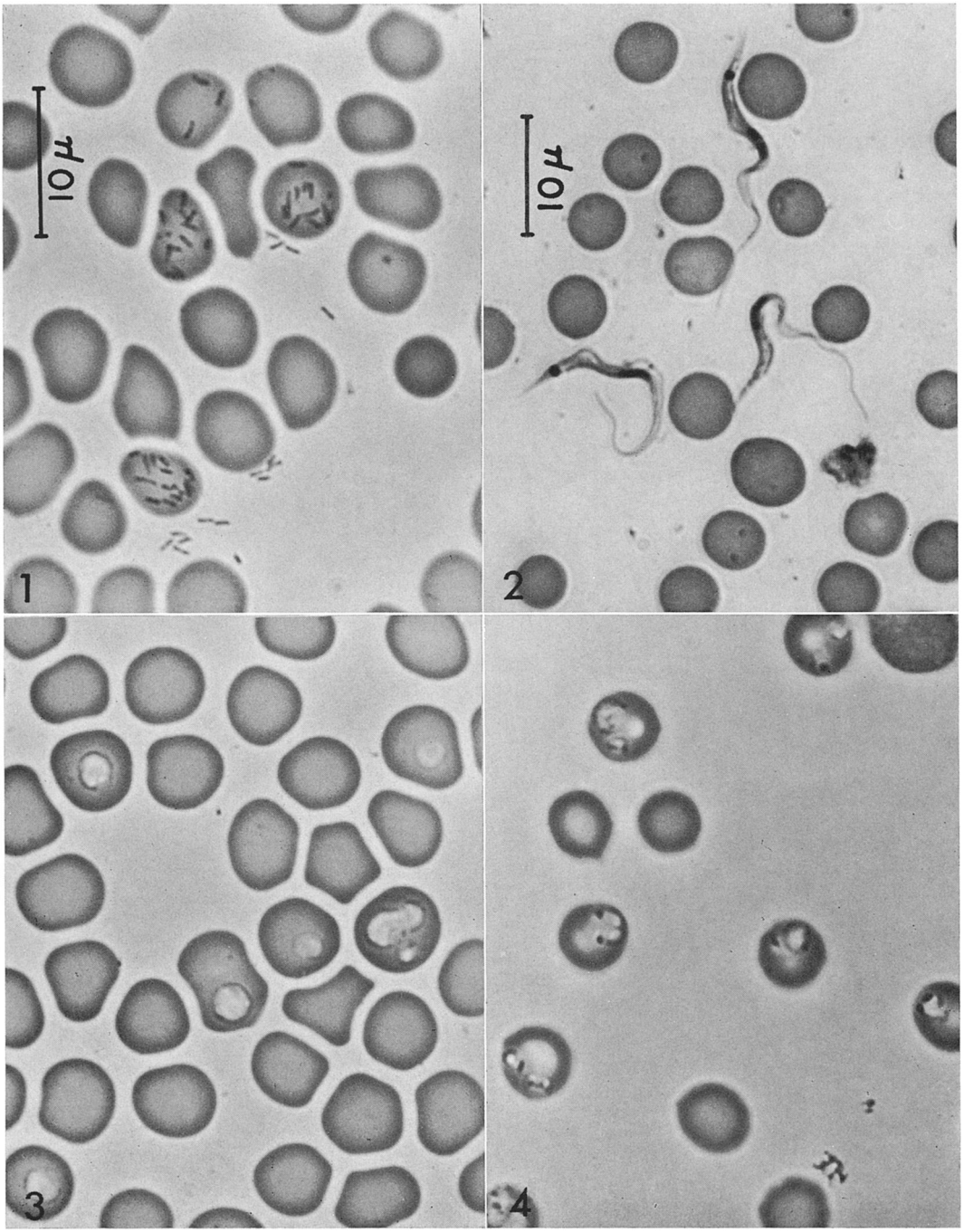
Trypanosomes

In the blood of one of six northern voles, captured alive at Lower Ugashik Lake on 10 October 1965, were found trypanosomes referable to the *T. lewisi* group (Fig. 2). These occurred in smears of peripheral blood at the rate of 2/1,000 rbc (about 20,000/ml) for the first 18 days after capture of the host, then declined gradually to about 0.2/1,000 rbc by the 48th day. None was found in smears prepared on the 54th day or at any time during the succeeding 18 months. Attempts to propagate the organism by inoculation of blood from the infected animal to laboratory-reared voles on the 54th day were unsuccessful.

Twenty-five trypanosomes from a smear prepared on 12 October were measured from camera lucida tracings, after the method utilized by Davis (1952). The dimensions of these were as follows: length overall 22.9 to 27.1 μ (mean $\pm$ standard error $= 24.84 \pm 0.23$ μ); distance from posterior tip to kinetoplast 3 to 3.5 μ; kinetoplast to center of nucleus 6 to 8 μ; center of nucleus to anterior end of body 8 to 10 μ; length of free flagellum 7 to 9 μ; width of body 1.5 to 2 μ; length of nucleus 1.5 to 3 μ; width of nucleus 0.5 to 1 μ. These were comparatively small organisms, with a smaller nucleus and longer flagellum than most of the recorded members of the *T. lewisi* group (cf. Lavier, 1921; Davis, 1952; Baker et al., 1963). Although they did not closely conform to trypanosomes designated as *T. microti* Laveran et Petit, 1909, for example, by Krampitz (1961), they are referable to that species on the basis of host occurrence. *T. microti* is believed to be host-specific in voles of the genus *Microtus* (Levine, 1965).

Piroplasms

Intraerythrocytic forms of a piroplasm were first detected by us in smears of blood and spleen from northern voles captured at Lower Ugashik Lake in October 1965. Subsequently, comparable organisms were found in northern voles from Amak Island, near the western end of the Alaska Peninsula, and in meadow voles, *Microtus pennsylvanicus* Ord, and northern red-backed voles, *Clethrionomys rutilus* Pallas, from the vicinity of Anchorage. By means of intraperitoneal inoculations with citrated blood and suspensions of splenic tissue, from naturally infected northern voles and northern red-backed voles, we successfully passed the organisms to laboratory-reared arvicoline rodents of the same and several other species (Table I.) The organism from northern voles taken near Ugashik Lake was isolated in laboratory-reared voles of the same subspecies, *M. o.*



operarius (Nelson), the original stock of which was obtained near Homer, Kenai Peninsula. It has been maintained for more than 3 years by serial passage in the laboratory colony of these voles. The isolate from the red-backed voles has been maintained in a laboratory colony of *C. r. dawsoni* (Merriam), the original stock of which was captured in the Anchorage area. These two piroplasms, designated by us as "strains" MO-U and CR-A,

TABLE I. *Results of experimental inoculations of laboratory-reared rodents*[1] *with citrated blood of voles harboring piroplasms.*[2]

Recipients	Origin of breeding stock	Number of animals infected per number inoculated with each piroplasm strain	
		Strain MO-U	Strain CR-A
Microtus oeconomus operarius	Ugashik Lake	15/17	4/4
Microtus oeconomus operarius	Homer	25/25	20/22
Microtus oeconomus innuitus	St. Lawrence I.	11/11	0/1
Microtus gregalis muriei	Umiat	3/3	–
Microtus abbreviatus fischeri	St. Matthew I.	–	3/3
Clethrionomys rutilus dawsoni	Anchorage	0/11	40/42
Lemmus sibiricus alascensis	Pt. Barrow	15/18	2/4
Dicrostonyx groenlandicus rubricatus	Pt. Barrow x Anaktuvuk Pass	5/6	–
Dicrostonyx groenlandicus stevensoni	Umnak Island	6/7	4/4
Peromyscus maniculatus osgoodi	Jamestown, North Dakota	0/4	0/4
Mus musculus (HA/ICR)	Laboratory[3]	0/3	–
Sigmodon hispidus ssp.	Laboratory[4]	0/1	–

[1] Also inoculated with the MO-U strain were two *C. rutilus dawsoni* and one *Ondatra zibethicus* (L.) live-trapped in the Fairbanks area. The two voles became infected but the muskrat did not.

[2] Donors: Strain MO-U, *Microtus oeconomus operarius* (Ugashik and Homer origins), Strain CR-A, *Clethrionomys rutilus dawsoni* (Anchorage origin).

[3] Original stock from Roswell Park Memorial Institute, Buffalo, New York.

[4] From Communicable Disease Center, Atlanta, Georgia; origin of stock unknown.

respectively, are morphologically similar but biologically different, as indicated by our negative results from repeated efforts to pass strain MO-U to red-backed voles of Anchorage origin, in which strain CR-A develops readily.

The early-stage parasitemia in laboratory-reared northern voles of Ugashik Lake and Homer lineages, inoculated with strain MO-U, was characterized by an exponential increase in rate of infection of erythrocytes up to the 9th or 10th day postinoculation. This was followed by a rapid decline to a very low level, which was sustained throughout the chronic phase of the infection. Maximal rates of infection of the erythrocytes ranged from 25 to 60% in the acute phase, which was further characterized by pseudomacrocytic anemia, oligocythemia, icterus, and splenomegaly. The anemia, oligocythemia, and icterus decreased gradually in intensity following the acute phase, whereas the splenomegaly persisted unchanged in the chronic phase.

Throughout the course of the infection, most of the affected erythrocytes in the peripheral blood harbored only a single piroplasm, usually of the circular or ring form (Fig. 3). The largest of these was about 3 μ in diameter. Oval, piriform, and rod-shaped organisms were uncommon to rare; anaplasmalike forms occurred in 0.1 to 5% of the infected cells. We found no clear signs of intraerythrocytic fission at any stage of the infection, but did find a few organisms whose form was suggestive of this kind of reproduction. For example,

←

FIGURES 1–4. Parasites in the blood of northern voles, *Microtus oeconomus*. **1.** Intra- and extra-erythrocytic *Grahamella*-like bodies in a laboratory-reared *M. o. operarius* (Homer origin), 17 days after inoculation with a suspension of ground fleas from wild voles of the same subspecies (Ugashik Lakes origin). **2.** Trypanosomes in a naturally infected *M. o. operarius*, 14 days after capture in the Ugashik Lakes district. This animal also harbored naturally acquired piroplasms (strain MO-U) and showed pseudomacrocytic anemia. **3.** Piroplasms of the MO-U strain, 8 days postinoculation in a laboratory-reared *M. o. operarius* (Homer origin), showing the intraerythrocytic ring form that predominates in all stages of the parasitemia in voles of that subspecies. A discontinuous band of nuclear chromatin is evident at the periphery of the otherwise vesicular parasites. Erythrocyte at right center contains two piroplasms of unequal size, the larger of which may be in the process of division. (Scale as in Figure 1.) **4.** Intraerythrocytic fission and multiple forms of piroplasms of the MO-U strain in an "atypical" host, a laboratory-reared St. Lawrence Island vole, *M. o. innuitus*, 10 days postinoculation. (Scale as in Figure 1.)

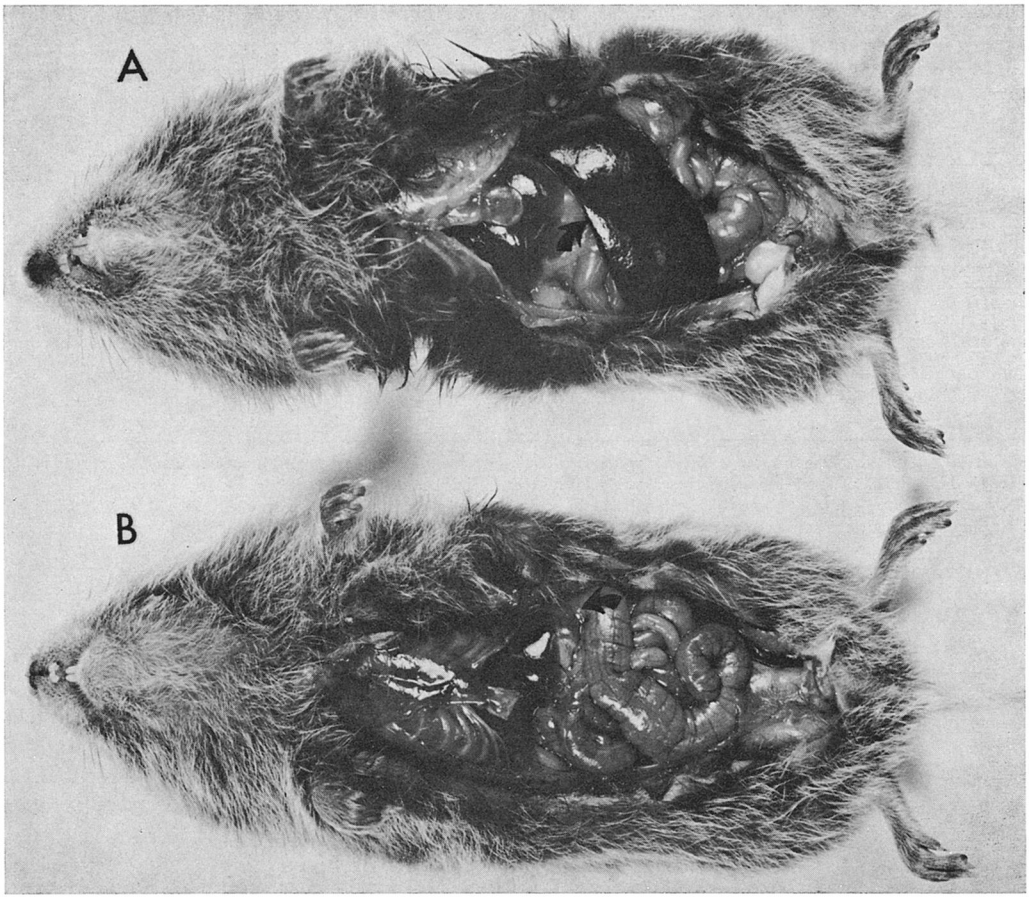


FIGURE 5. Piroplasm-induced splenomegaly in a northern vole, *Microtus oeconomus*, 14 days post-inoculation. The enlarged spleen (arrow) of the infected animal (A) extends diagonally across the abdomen, while that of its normal sibling (B) lies hidden from view in its usual position laterodorsal to the stomach (arrow). The spleen of the infected animal had a volume approximately 46 times greater than that of the normal individual.

in 1,362 infected erythrocytes from four northern voles in the exponential stage (6th to 9th day) of the developing parasitemia, 1,338 cells (98.3%) contained only single parasites, 11 of which seemed to be partly constricted, as if undergoing division. In only three of these were the two parts approximately equal in size; in the rest they were very unequal. Twenty-two infected cells contained two ring forms, mostly unequal in size; one contained a ring and an anaplasmalike form, and one contained what appeared to be a tetrad, though not of the classic "maltese cross" form. From these findings we judge that intraerythrocytic fission is, at most, uncommon to rare and is not the principal means of reproduction in the normal vertebrate host. The principal reproductive process may be schizogony; extracellular forms of the parasite were abundant in the spleen and bone marrow and some clumps of these resembled schizonts.

Intraerythrocytic fission was, however, a very common method of reproduction in the "atypical hosts," the voles and lemmings from arctic and insular localities in which these piroplasms apparently do not occur (see below). Diads, tetrads, and extracellular forms were abundant in the peripheral blood of these animals (Fig. 4), and a much greater proportion of the erythrocytes was invaded by the parasites, approaching 100% in the acute stage of the disease. The anemia and icterus

TABLE II. *Species of arvicoline rodents in which splenomegaly has been recorded and localities where splenomegalous individuals were captured.*

Species	Localities[1]
Clethrionomys rutilus	Cold Bay, Ugashik Lakes, Kukak Bay,[2] Anchorage, Talkeetna, Nabesna, Valdez, Yakataga
Microtus pennsylvanicus	Anchorage
Microtus oeconomus	Cold Bay, Amak Island, Ugashik Lakes, Becharof Lake, Kukak Bay,[2] Kodiak, Homer, Kenai, Sterling, Hope, Portage, Anchorage, Palmer, Talkeetna, Chilkat Pass (Yukon Territory, Canada)
Microtus gregalis	Palmer Creek (near Hope)
Lemmus sibiricus	Ugashik Lakes, Becharof Lake
Synaptomys borealis	Kenai, Portage
Dicrostronyx groenlandicus	Umnak Island

[1] All localities are "Alaska" except as indicated.
[2] Specimens collected by E. L. Schiller (Schiller and Rausch, 1956).

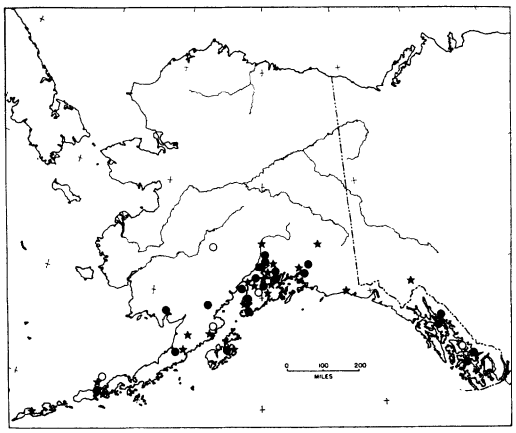


FIGURE 6. Geographical distribution of records of splenomegalous rodents and of ticks, *Ixodes angustus*, in Alaska and adjacent Canada. The rodents are indicated by stars. Published records of *I. angustus* (open circles) are those of Cooley and Kohls (1945) and Schiller and Rausch (1956); new records (solid dots) are summarized in Table III. Multiple records from one locality are represented by single symbols.

also were more extreme than in the normal hosts and were accompanied by severe hematuria and general debilitation. Whereas none of the voles of Ugashik and Homer origins died as a result of the infection, the voles and lemmings from outside the enzootic area usually died before the 15th day postinoculation.

Splenomegaly is pathognomonic for the infection in the natural hosts, since it persists in the chronic stage of the disease for the duration of life of the animal. The increased volume of the spleen, usually about 40 times that in the noninfected animal, is readily apparent and easily recognized in wild-trapped rodents (Fig. 5). We have recorded it in seven species of arvicoline rodents from 20 localities in southern Alaska and adjacent Canada (Table II). The absence of splenomegaly in several thousand rodents of the same species from western, central, and northern Alaska is taken as evidence of the absence of piroplasms in those areas.

Hematozoa of the order Piroplasmida Wenyon, 1926, are dependent on ixodid ticks as vectors, insofar as is known. Since *Ixodes angustus* is the only species of tick we have found on arvicoline rodents in Alaska, we consider it the most probable vector of the organisms described here. Circumstantial evidence in support of this is found in the coincidence of the known distribution of *I. angustus* with that of splenomegalous rodents (Table III, Fig. 6). In addition, we have successfully transmitted organisms of strain MO-U from vole to vole via ticks of this species, reared in the laboratory. Larval ticks, engorged on an experimentally infected vole, transmitted the organism to other laboratory-reared voles on which they fed as nymphs. However, transovarial transmission from a naturally infected adult tick to its larvae did not occur, as evidenced by failure of such larvae to infect susceptible voles. Although *I. angustus* occurs widely on mammals in northern North America and northeastern Eurasia (Cooley and Kohls, 1945; Pomerantsev, 1950; Gregson, 1956), ticks of this species have not been implicated previously in the transmission of any pathogen. Further investigation of the role of *I. angustus* in the transmission of these piroplasms is under way in our laboratory.

The piroplasms reported previously from small rodents, e.g., by França (1912), Coles (1914), Yakimoff and Saphronowitsch (1917), and Shortt and Blackie (1965), were assigned to several genera: *Smithia* França, 1909, *Nuttallia* França, 1909, *Theileria* Bettencourt,

TABLE III. *New distribution records of* Ixodes angustus *in Alaska.*

Locality	Date	Host	Collector or authority[1]
Amak Island	4–5 Jun. 1968	*Microtus oeconomus*	FHF
Cold Bay	8 Jun. 1968	*Clethrionomys rutilus*	FHF
Ugashik Lakes	6–7 Oct. 1963	*Lemmus sibiricus*, *M. oeconomus*	RLR
Dillingham	30 Jun. 1958	*C. rutilus*	FHF
Iliamna Lake	28 May 1958	*C. rutilus*	FSLW
Kodiak Island	13 Jun. 1951	*M. oeconomus*	RLR
Kalgin Island	20 May 1952	*Tamiasciurus hudsonicus*	RLR
Anchor River	9 Jun. 1954	*M. oeconomus*	RLR
Seldovia	19 Jun. 1954	*T. hudsonicus*	DKH
Daniel's Lake	15 Jul. 1952	*C. rutilus*	RLR
Hope	23 Aug. 1952	*T. hudsonicus*	RLR
Goose Bay	9 Jun. 1948	*Sorex* sp.	JDG
Cottonwood Creek	10 Jun. 1948	*C. rutilus*	JDG
Hatcher Pass	24 Jul. 1952	*Microtus* sp.	RLR
Archangel Creek	30 May 1954	*Ochotona collaris*	RLR
Palmer	May 1951	*C. rutilus*	RLR
Peters Creek	16, 18 Aug. 1951	*Microtus* sp., *C. rutilus*	RLR
Fort Richardson	18 Aug. 1948	*Sorex* sp.	JDG
Anchorage	19 May 1955, 13 Jul. 1956	*C. rutilus*	RLR
Anchorage	19 Jul. 1960	*M. oeconomus*	MV
Potter	28 Jun. 1957	*C. rutilus*	RLR
Portage	2 Jul. 1961	*Sorex obscurus*	RLR
Valdez	8–12 Jul. 1948	*Sorex* sp., *C. rutilus*	JDG
Valdez	20 Jul. 1959	*Microtus* sp.	ELK
Thompson Pass	13 Jul. 1948	*O. collaris*	JDG
Thompson Pass	8 Jul. 1961	*M. oeconomus*	RLR
Juneau	4 Oct. 1945, 29 Aug. 1948, 1–2 Apr. 1950, 17 Sep. 1949	*T. hudsonicus*	GMK
Juneau	22 May 1961	Domestic dog	GMK
Douglas Island	5 Sep. 1949	*T. hudsonicus*	GMK
Prince of Wales I.	23 May 1962	*Peromyscus maniculatus*	GMK
Wrangell Island	1, 8, 24 Apr. 1946, 6 Jun. 1946	*T. hudsonicus*	GMK
Wrangell	26 Mar. 1946	*T. hudsonicus*	GMK
Wrangell	24 Apr. 1946	Man (on clothing)	GMK

[1] F. H. Fay, J. D. Gregson, D. K. Hilliard, E. L. Karlstrom, G. M. Kohls, R. L. Rausch, M. Voge, F. S. L. Williamson.

França, and Borges, 1907, and *Babesia* Starcovici, 1893, principally on the basis of the form of the intraerythrocytic stages and host occurrence, neither of which is adequate for generic determination (Neitz, 1965). For the present, we have chosen not to assign the organisms that we have found to any genus, since the taxonomy of the Piroplasmida is currently uncertain, and the diagnostic value of previously accepted morphological and biological characters of "genera" and "species" is now in doubt (Neitz, 1965). Further uncertainty about the validity of those characters is raised by the contrasting performances of the MO-U strain in normal versus atypical hosts.

The majority of genera and species of piroplasms has been described from domestic animals, rather than from wild mammalian hosts. Conceivably, their structure and development in the former are atypical and more variable than in the natural hosts. The piroplasms of wild animals are little known, and their biology and enzootiology poorly understood. The finding of two kinds of these organisms, which can readily be studied in the field as well as reared in their normal hosts and hosts of several other species in the laboratory, should facilitate the acquisition of basic information for solution of some of these problems.

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